

## CROSS DIFFUSION AND COEXISTENCE OF TWO SPECIES ON A GRADIENT

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**ABSTRACT.** Starting from observations on an apparent replacement process between two closely related bird species, the problem of joint diffusion of two species is studied in terms of a cross diffusion model, without any competitive interaction. It is assumed that each species observes (or reacts to) the joint gradient and that the joint population follows the linear diffusion equation. Under this realistic hypothesis the density of each individual species is governed by a highly non-linear diffusion equation, and this dynamics favors the species which is less evenly distributed. In particular, in regions where the domains of both species overlap, i.e., where reservoirs stabilize clines, the species with the steeper gradient has an advantage. This effect is studied in greater detail.

**Introduction** There is a vast number of publications on so-called cross diffusion, in particular with respect to applications—or interpretations—in ecology, beginning with [14] and [2, 3, 11], and further [6, 9, 7, 8, 10, 16, 18, 19], and many others. In [1] the solutions of equations with cross-diffusion are compared to and approximated by the solutions of reaction diffusion equations. In many of these papers classical ecological models such as prey-predator or Volterra competitive dynamics are supplemented with diffusion terms whereby the diffusion rates depend on the densities of the species. The resulting systems are used to incorporate into the classical models additional effects like crowding. It appears that pure cross diffusion, without reaction terms, has not been studied to that extent, although there seem to exist quite interesting effects which may be also relevant in ecology.

The present study has been stimulated by a recent paper by Koonce [4] who tried to explain the replacement process between two species of warblers  $B$  (blue-winged) and  $G$  (golden-winged), which has been observed in the field, by a computer-based model with juvenile dispersal and differential ability to occupy habitat. The details of the model

are not important for the present study. Koonce models the juvenile dispersal process by a discrete system

$$B_i^{new} - B_i = \frac{(B+G)_{i+1}B_{i+1}}{(B+G)_{i+1} + (B+G)_i} + \frac{(B+G)_{i-1}B_{i-1}}{(B+G)_i + (B+G)_{i-1}} - \frac{(B+G)_iB_i}{(B+G)_{i+1} + (B+G)_i} - \frac{(B+G)_iB_i}{(B+G)_i + (B+G)_{i-1}}$$

which can be seen as a discrete version of a system for species  $v$  and  $w$  which move according to the following density dependent cross diffusion law,

$$(1) \quad \begin{aligned} v_t &= \left( \frac{((v+w)v)_x}{2(v+w)} \right)_x \\ w_t &= \left( \frac{((v+w)w)_x}{2(v+w)} \right)_x. \end{aligned}$$

The motivation to study this non-linear system becomes obvious if one looks at the total density  $u = v + w$  which satisfies

$$u_t = \left( \frac{(u^2)_x}{2u} \right)_x = u_{xx}.$$

In (1) the solution of the linear diffusion equation is split with respect to two types. Of course there are many possible splits of the form (' denotes the derivative with respect to  $u$ )

$$(2) \quad v_t = \left( \frac{(\phi(u)v)_x}{(\phi(u)u)'} \right)_x, \quad w_t = \left( \frac{(\phi(u)w)_x}{(\phi(u)u)'} \right)_x$$

such that each species observes the same weighted gradient of the total population. Then  $\phi(u) \equiv 1$  is the linear case and  $\phi(u) = u$  corresponds to (1). Hence the system (1) appears as the simplest non-linear split which is suited to explain the observed phenomenon. The generalization to more than two types is straightforward and will not be presented here.

The corresponding system in several space dimensions reads

$$(3) \quad \begin{aligned} u_t &= \Delta u \\ v_t &= \nabla \cdot \left( \frac{\nabla(uv)}{2u} \right) \\ w_t &= \nabla \cdot \left( \frac{\nabla(uw)}{2u} \right) \end{aligned}$$

where the inner  $\nabla$  is the gradient and the outer  $\nabla$  is the divergence. Notice that this system makes sense only for positive total density  $u$ . Difficulties arise if initial data  $u = v + w$  are somewhere zero. Hence this system will not be suited to model invasion of two species  $v$  and  $w$  into some empty habitat but rather for invasion of one species into the habitat of the other as in the replacement process of bird species.

Although the densities of the individual species satisfy nonlinear equations, their sum satisfies a linear diffusion equation. If one of the two species is absent, say  $w \equiv 0$ , then the other species  $v$  satisfies the linear diffusion equation  $v_t = \Delta v$ . If the total density is constant then  $v$  and  $w$  satisfy the linear diffusion equation separately.

This system has several mathematical properties which lead to ecological insights on densities in unevenly distributed populations.

**1 Qualitative properties of the system** We check whether the system (3) is a parabolic system (and hence qualifies as a standard evolution equation). We expand

$$\begin{pmatrix} v \\ w \end{pmatrix}_t = \begin{pmatrix} 1 + \frac{v}{v+w} & \frac{v}{v+w} \\ \frac{w}{v+w} & 1 + \frac{w}{v+w} \end{pmatrix} \begin{pmatrix} \Delta v \\ \Delta w \end{pmatrix} + \dots$$

where  $\dots$  indicates terms which contain only first order derivatives. We see that the diffusion matrix is symmetrizable, it has trace 3 and determinant 2, the eigenvalues are 2 and 1. Hence the system is indeed parabolic.

The system (3) can be solved by solving three linear problems in succession, first the equation for  $u$  and then those for  $v$  and  $w$ . Hence there are no problems with respect to existence and uniqueness of solutions as long as  $u$  is positive. Positivity of  $u$  for all times can be ensured by non-negative initial data and non-negative prescribed boundary data or no-flux data such that not all these data vanish identically.

The equation for  $v$  in (3) can also be written

$$(4) \quad v_t = \frac{1}{2}\Delta v + \frac{1}{2}\nabla((\nabla \log u)v),$$

similarly the equation for  $w$ . In this form the equation says that the  $v$  particles are subject to Brownian motion and also to convection whereby they follow the logarithmic gradient of the total population  $u$ . Diffusion terms of the form  $\nabla(u\nabla(\log u))$  have also been used in chemotaxis modeling [5, 12].

The equation for  $v$  in (3) can be written in yet another form which will be useful in the sequel,

$$(5) \quad v_t = \Delta v + \frac{\nabla u \cdot \nabla v}{u} - \frac{v}{u^2}(\nabla u)^2 + \frac{v}{u}\Delta u.$$

Following the ecological interpretation, we study the system on a bounded domain  $\Omega$  with fixed densities on the boundary (Dirichlet boundary conditions)

$$\begin{aligned} v(x) &= \phi(x), & w(x) &= \psi(x), & x &\in \partial\Omega, \\ u(x) &= \phi(x) + \psi(x), & x &\in \partial\Omega. \end{aligned}$$

In general, the boundary data  $\phi, \psi$  will not be constant, we assume that  $\phi, \psi \geq 0$  and that  $\phi + \psi$  is everywhere positive.

We look for stationary solutions. In the stationary case  $\Delta u = 0$ , the function  $u$  is a harmonic function, hence it cannot have strict maxima or minima in the interior of the domain  $\Omega$ . The functions  $v, w$  are non-negative everywhere. From equation (5) we have the stationary equation for  $v$ ,

$$(6) \quad \Delta v + \frac{\nabla u \cdot \nabla v}{u} - \frac{v}{u^2}(\nabla u)^2 = 0.$$

**Proposition 1.** *Let the function  $v$  be continuous in  $\overline{\Omega}$  and twice differentiable in  $\Omega$ . Let  $v$  be a solution of equation (6) in  $\Omega$ . Then*

$$(7) \quad \max_{x \in \overline{\Omega}} v(x) = \max_{x \in \partial\Omega} v(x).$$

*Furthermore, unless  $v$  is constant,  $v$  cannot have a strict interior maximum. For the function  $w$  analogous statements hold.*

*Proof.* In equation (6) we have  $v(\nabla u)^2/u^2 \geq 0$  and hence the standard maximum principle applies (see [13, 17]).  $\square$

In particular, if the function  $v$  has an extremum in the interior of the domain  $\Omega$ , then  $\nabla v = 0$  and

$$\Delta v = \frac{v}{u^2}(\nabla u)^2 \geq 0$$

indicating that the extremum is a minimum.

The special case where one of the two species, say  $v$ , is constant on the boundary, shows a clear effect on the density of that species.

**Proposition 2.** *If the function  $\phi$  is constant and  $\psi$  is not constant then*

$$v(x) < \phi, \quad x \in \Omega,$$

*and  $v$  has an interior minimum but no interior maxima.*

In ecological terms the proposition says the following: Suppose the species  $v$  is constant on the boundary. If the species  $w$  is absent, then the species  $v$  is constant throughout the domain. On the other hand assume that the species  $w$  is not constant on the boundary. If  $v$  is absent, then  $w$  will be a non-constant solution of the Laplace equation. If both species live together, then  $v$  loses population in every case, whatever the boundary data of  $w$  are.

Now we look at proportions  $p = v/u$  and  $q = w/u$ . From the equation (5) we get an equation for the proportion  $p$ ,

$$(8) \quad p_t = \frac{1}{u} \Delta p + 3 \frac{\nabla u}{u} \cdot \nabla p + 2 \frac{\Delta u}{u} p.$$

Again we study the stationary problem. We find the following.

**Proposition 3.** *In the stationary situation none of the functions  $p$  and  $q$  can have a strict minimum or maximum.*

*Proof.* In view of  $\Delta u = 0$  the function  $p$  satisfies the linear equation

$$\Delta p + 3 \nabla u \cdot \nabla p = 0.$$

Then the proof follows by standard arguments [13, 17].  $\square$

We observe that the density  $v$  can have a local minimum (if  $\phi$  is constant then it has a local minimum) while the proportion  $p$  cannot have a local minimum. It follows that a local minimum of  $v$  is located in an area where the density  $u$  is low. This statement can be made more precise in the case of space dimension 1 in terms of monotony and convexity.

**2 Space dimension 1** In the case of one space dimension the features exhibited so far can be described in quantitative terms. Let  $\Omega$  be the interval  $(0, l)$  and let the Dirichlet boundary conditions be given by

$$(9) \quad \begin{aligned} v(0) &= v_0, & v(l) &= v_1 \\ w(0) &= w_0, & w(l) &= w_1 \end{aligned}$$

with  $v_0, w_0, v_1, w_1 \geq 0$ . Let

$$u_0 = v_0 + w_0, \quad u_1 = v_1 + w_1$$

with  $u_0, u_1 > 0$ . Since  $u$  satisfies the linear diffusion equation, we have

$$(10) \quad u(x) = v(x) + w(x) = (v_1 + w_1)\frac{x}{l} + (v_0 + w_0)\left(1 - \frac{x}{l}\right).$$

**Proposition 4.** *Consider the stationary situation. For any choice of the boundary data the  $v$  component of the solution has the explicit representation*

$$(11) \quad v(x) = \frac{(v_1 u_1 - v_0 u_0)[u_1(\frac{x}{l})^2 - u_0(1 - \frac{x}{l})^2] + u_0(v_0 + v_1)u_1}{(u_0 + u_1)[u_1(\frac{x}{l}) + u_0(1 - \frac{x}{l})]}.$$

*Proof.* Integrating the stationary  $v$  equation, we find  $(uv)_x = 2du$  with  $d$  yet unknown. With (10) we get

$$(uv)_x = 2\frac{d}{l}(u_1 x + u_0(l - x)).$$

Integrating again, we find

$$uv = \frac{d}{l}(u_1 x^2 - u_0(l - x)^2) + c$$

with  $c$  yet unknown. Hence we have, again with (10),

$$v(x) = \frac{d(u_1 x^2 - u_0(l - x)^2) + c}{u_1 x + u_0(l - x)}$$

with two unknown parameters  $c$  and  $d$  to be determined from the boundary conditions for  $v$ ,

$$v_0 = \frac{-du_0 l + c}{u_0}, \quad v_1 = \frac{du_1 l + c}{u_1},$$

from where

$$d = \frac{v_1 u_1 - v_0 u_0}{(u_0 + u_1)l}, \quad c = \frac{u_0 u_1 (v_0 + v_1)}{u_0 + u_1}.$$

Now (11) follows. □

This formula can be simplified if one distinguishes the cases  $u_0 = u_1$  and  $u_0 \neq u_1$ . Recall that for a stationary solution the function  $u(x)$  is linear.

**Proposition 5.** *Assume the stationary situation.*

i) *If  $u_0 = u_1$ , then (11) simplifies to*

$$v(x) = \left(\frac{x}{l}\right)v_1 + \left(1 - \frac{x}{l}\right)v_0$$

*which says that if the total population is constant in space then  $v$  and  $w$  have the standard linear shape.*

ii) *If  $u_0 \neq u_1$ , then (11) can be written as*

$$(12) \quad v(x) = \frac{(v_1u_1 - v_0u_0)u^2(x) + u_0u_1(u_1v_0 - u_0v_1)}{(u_1^2 - u_0^2)u(x)}.$$

*Proof.* By elementary algebra

$$(u_1 - u_0) \left[ u_1 \left( \frac{x}{l} \right) - u_0 \left( 1 - \frac{x}{l} \right) \right]^2 = \left[ u_1 \left( \frac{x}{l} \right) + u_0 \left( 1 - \frac{x}{l} \right) \right]^2 - u_0u_1.$$

For ii) use the above formula to replace the square bracket in the numerator of formula (11).  $\square$

The formula (12) shows that  $v(x)$  and  $w(x)$  are rational functions of  $u(x)$ ,

$$v = au + \frac{b}{u}, \quad w = (1 - a)u - \frac{b}{u}$$

with the coefficients  $a$  and  $b$  depending on the boundary data,

$$(13) \quad a = \frac{v_1u_1 - v_0u_0}{u_1^2 - u_0^2} = \frac{u_0v_0}{u_1^2 - u_0^2} \left( \frac{u_1}{u_0} \frac{v_1}{v_0} - 1 \right),$$

$$b = \frac{u_0u_1(u_1v_0 - u_0v_1)}{u_1^2 - u_0^2} = \frac{u_0^2u_1v_0}{u_1^2 - u_0^2} \left( \frac{u_1}{u_0} - \frac{v_1}{v_0} \right).$$

We study the qualitative properties of the functions  $v$  and  $w$  in terms of  $a$  and  $b$  as given in (13). The case  $a < 0$ ,  $b < 0$  is impossible in view of the assumptions.

**Proposition 6.** *Let  $u_0 < u_1$ . (The case  $u_0 > u_1$  is similar.)*

- i) The function  $v(x)$  is strictly convex if  $b > 0$  and strictly concave if  $b < 0$ .  
 ii) The function  $v(x)$  is strictly increasing if either

$$b < 0, \quad a > 0,$$

or

$$b > 0, \quad au_0^2 > b.$$

- iii) If  $b > 0$  and  $a > 0$  and furthermore  $u_0^2 < b/a < u_1^2$ , i.e.,

$$(14) \quad u_0^2 < \frac{u_0 u_1 (u_1 v_0 - u_0 v_1)}{u_1 v_1 - u_0 v_0} < u_1^2,$$

then (and only then) the function  $v(x)$  has a minimum  $\bar{u}$  in  $(0, l)$ . The minimum is located at the position where the function  $u$  has the value  $\bar{u} = \sqrt{b/a}$ . This value is assumed at the position

$$\bar{x} = l \frac{\bar{u} - u_0}{u_1 - u_0}.$$

*Proof.* Follows by straightforward computation.  $\square$

The condition (14) can also be written in terms of proportions

$$1 < \frac{u_1}{u_0} \left( \frac{\frac{u_1 - v_1}{u_0} - \frac{v_1}{v_0}}{\frac{u_1 v_1}{u_0 v_0} - 1} \right) < \left( \frac{u_1}{u_0} \right)^2.$$

**Corollary 1.** *Whenever*

$$(15) \quad \left( \frac{v_1}{u_1} - \frac{v_0}{u_0} \right) (u_1 - u_0) < 0,$$

then

$$v(x) < \left( 1 - \frac{x}{l} \right) v_0 + \frac{x}{l} v_1,$$

i.e.,  $v$  is worse off than it would be in the absence of  $w$ .

*Proof.* If  $u_0 < u_1$  then by i) the function  $v$  is convex if the coefficient  $b$  is positive. The inequality expresses just this fact, including the case where  $u_0 > u_1$ .  $\square$



In particular, for  $v_0 = v_1 = \phi$  we can get an explicit version of Proposition 2. We find

$$(16) \quad \begin{aligned} a &= \bar{v} \frac{1}{u_0 + u_1}, & b &= \bar{v} \frac{u_0 u_1}{u_0 + u_1} \\ v(x) &= \phi V(x), & V(x) &= \frac{u^2(x) + u_0 u_1}{(u_1 + u_0)u(x)}. \end{aligned}$$

which has a minimum at

$$\bar{x} = \frac{\sqrt{u_0 u_1} - u_0}{u_1 - u_0};$$

the minimal value is

$$V(\bar{x}) = \frac{2\sqrt{u_0 u_1}}{u_0 + u_1} < 1.$$

Hence if the  $v$  species is constant on the boundary and the  $w$  species has a steep gradient, then  $v(x)$  is convex and has a strict internal minimum while  $w(x)$  is concave. In particular, the total population size of  $v$  is less than it would be in the absence of  $w$  and the total population size  $w$  is greater than it would be in the absence of  $v$ .

The flux of  $v$  through the boundary can be computed (for constant  $\phi$ ) as

$$\phi \frac{u_1 - u_0}{u_1 + u_0} = \phi \frac{w_1 - w_0}{w_1 + w_0 + 2\phi}.$$

If the species  $w$  were absent then  $v$  would be constant and the flux through the boundary would be zero. In the presence of  $w$  there is a flux of  $v$  through the boundary but nevertheless  $v$  is replaced by  $w$  to some extent in the interior.

We consider two scenarios which come close to the bird replacement problem. Suppose that the  $v$  species resides below the interval  $[0, l]$  and the  $w$  species above, i.e.,  $v_0 > 0, v_1 = 0$  and  $w_0 = 0, w_1 > 0$  whereby  $w$  has a higher density in its exclusive domain as compared to  $v$  in its domain, i.e.,  $v_0 < w_1$ . Then  $u_0 < u_1, a < 0, b > 0$ .

We can reduce the number of parameters by normalizing the length of the interval to  $l = 1$ , and by choosing  $v_0 = 1$  and  $w_1 = 1 + \sigma$  with  $\sigma > 0$ . The function  $v(x)$  is decreasing and convex while  $w$  is increasing and concave. At each space point the density  $v(x)$  is smaller as compared to the situation where  $w$  is absent, see Figure 1. Correspondingly, the density of  $w$  is higher than in the absence of  $v$ .

In the second scenario  $v$  is homogeneously distributed in the absence of  $w$ , and  $w$  shows a gradient in the absence of  $v$ . Then, whatever the actual values are,  $v$  loses and  $w$  gains, see Figure 2.

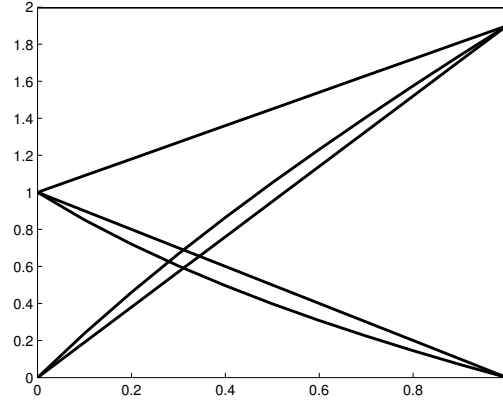


FIGURE 1: The species  $v$  lives in  $x < 0$  with  $v_0 = 1$ ,  $v_1 = 0$ , and the species  $w$  lives in  $x > 1$  with  $w_1 = 1 + \sigma$ ,  $\sigma = 0.9$ ,  $w_0 = 0$ . In the overlap area  $[0, 1]$  the density  $v(x)$  is a decreasing and convex function while the density  $w(x)$  is increasing and concave. Thus,  $w$  gains and  $v$  loses.

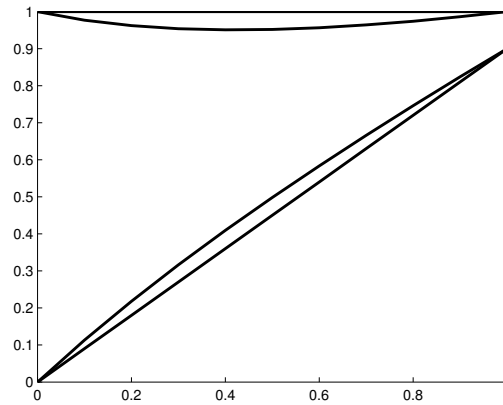


FIGURE 2: The species  $v$  is homogeneously distributed in  $[0, 1]$  with  $v_0 = v_1 = 1$  while  $w$  has a marked gradient,  $w_0 = 0$ ,  $w_1 = \rho$ ,  $\rho = 0.9$ . Then the density  $v$  is convex and the density of  $w$  is concave. The species  $w$  gains and the species  $v$  loses.

**3 Discussion** Suppose that two similar species with densities  $v$  and  $w$  “compete” in the way that each species adjusts to the joint population gradient. Then the equilibrium density of each species may be far off an equilibrium solution of the diffusion equation (in one space dimension far off a linear function). Suppose further that there are two disjoint domains such that each species is established exclusively in one domain. Then in the transitional zone between the two domains the species which has the steeper gradient (in the absence of the other species) has some advantage in terms of absolute local population size. The density of the species with the shallow gradient may even have a local minimum in the transitional zone.

The situation changes if one considers local relative frequency instead of absolute population size.

These findings support the views of Koonce and validate his discrete model. The approach via partial differential equations has the advantage that some relevant insights can be gained in terms of general principles and explicit formulas rather than by computer simulation.

We underline that the models presented in [4] and here are not based on direct competitive interaction as in Lotka-Volterra models and also not on indirect competition (via resources) as in the competitive exclusion principle or the chemostat. The general message is the following: In the overlap zone of two very similar species the species with the steeper gradient has an advantage, if both species adapt their local distribution to the *joint* density. In particular, if there is an incumbent species and an advancing species (whatever may cause the advance) then the advancing species has some numerical advantage over the resident species. The latter statement shows that we have to be careful with interpretations: The concavity or convexity of the profiles may be not the cause for the advance but rather a consequence.

In this interpretation the present model is a medium time scale snapshot of the wave front in a propagation model with a longer time scale.

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